THE EYES OF CAMBARUS SETOSUS AND CAMBARUS PELLUCIDUS.[1]

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Cambarus setosus Faxon inhabits the caves of southwestern Missouri. It was described by Faxon in Garman's account of the "Cave Animals of Southwestern Missouri." An account of the eyes of this species was published by Parker.

In June, 1911, I secured an abundance of fresh material which made a reëxamination of the eyes desirable. I found it in the caves about Springfield, Sarcoxie and Ozark, Missouri. From Smallen's cave near Ozark I secured seventy-five specimens from 20 to 110 mm. in length. In addition to these, twenty-seven specimens of *C. pellucidus testii* Hay were taken from Mayfield's cave near Bloomington, Indiana. Also thirty-three *C. pellucidus* (Tellkampf) from Shawnee cave, Indiana University farm, near Mitchell, Indiana. The specimens from Indiana were collected during the fall and winter of 1911 and 1912. The blind crayfish from Indiana are smaller than those from Missouri. The smallest taken from Indiana caves were 9 mm. in length. Others varied from 15 to 60 mm. The largest specimen of *C. setosus* taken was 120 mm. in length.

C. setosus has been found only west of the Mississippi river, while *C. pellucidus* has been found only east of the Mississippi both north and south of the Ohio river. *C. pellucidus testii* Hay has been recorded only from Mayfield's Cave, Bloomington, Indiana. *C. pellucidus* has probably the widest distribution of any of the blind crayfish. It has been taken from Mammoth and other caves of Kentucky and from Wyandotte and other caves in Crawford county, from Clifty cave, Washington county, from Lost river, Orange county, from Shiloh, Down's, Donnehue's

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and Donnelson's caves in Lawrence county, Indiana. Strong's, Truitt's, Kuntz's, Marengo, Little Wyandotte or Seibert's and several smaller caves of Indiana were examined for blind crayfish but none were found.

The caves of Indiana are in the same general geological forma-

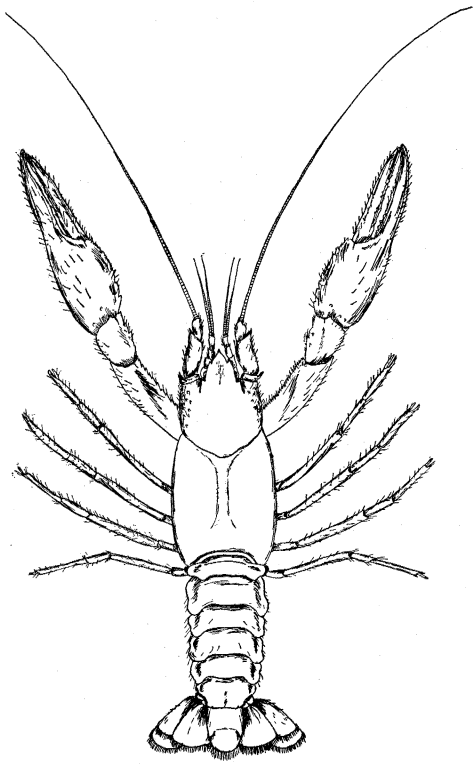
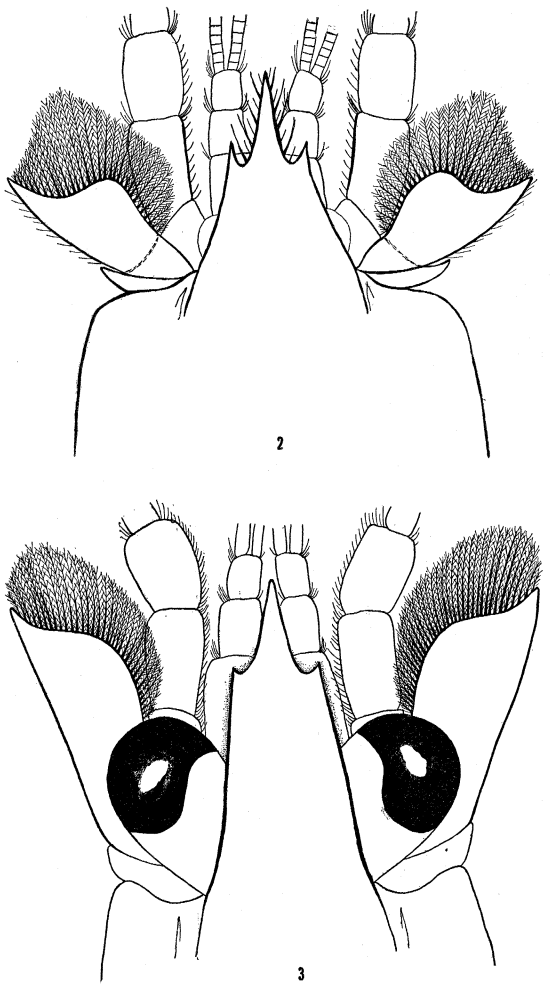


FIG. 1. Dorsal view of *C. setosus* 110 mm. long, with small, inconspicuous eyes extending slightly from under the rostrum. (Life size—reduced ½.) Drawn by Miss Dorothy L. VanDyke.

tion as those of Missouri. For an account of the Missouri caves see Shepard, in the Missouri Geological Survey, Vol. XII., 1898. For the fauna and geology of Indiana caves see Green, Indiana Academy of Science, 1908, and Blatchley, Indiana Department of Geology and Natural Resources, Twenty-first Annual Report, 1896.

The structure of the eyes in the blind crayfish, *C. pellucidus*, was first noted by Newport (1855). Concerning his specimens which were taken from Mammoth cave, Kentucky, he states:



FIGS. 2 AND 3. Dorsal views of the anterior ends of *C. setosus* and *C. propinquus*(?) 36 mm. long. They show the relative size and conspicuousness of the eyes of the two species.

"The hardened tegument which clothes the entire organ is thinnest and most transparent in that part of the eye which forms

the cornea in other Crustaceans; so that the eye may be unfitted for distinguishing form, the creature may yet possess the faculty of perceiving the small amount of actinic rays of light which might penetrate into its subterranean abode . . . ; the cornea also exhibits an appearance of being divided into a few imperfect corneals (facets) at the apex of the organ, and the structures behind these into chambers, to which a small but distinct optic nerve is given." He also noted that the eyes are not pigmented.

I find that the eyes of *C. pellucidus* from Indiana caves and of *C. setosus* from Missouri caves show neither "corneals" (facets) nor "chambers, to which a small but distinct optic nerve is given."

The next writer on the eyes of blind crayfish was Leydig (1883). He stated that the cornea in *C. pellucidus* is lamellated, without pigment and without facets. His description of the internal structures of the eye is very general and indefinite.

Packard (1888) in his memoir on "The Cave Fauna of North America" describes and illustrates the form and structure of the eyes of *C. pellucidus* from Indiana and Kentucky caves and *C. hamulatus* Cope and Packard from Nickajack cave, Tennessee. He found that in both species the cornea is without facets and that the hypodermis is of the same thickness in the retinal region as in other parts of the eye; also that the optic nerve and optic ganglion are present.

The following year (1889) Garman published Faxon's description of *C. setosus* to which reference was made in the opening paragraph.

Parker (1890) published a paper on "The Eyes in Blind Crayfishes." He had access to *C. hamulatus* and *C. setosus*. The major part of his paper deals with *C. setosus*. He emphasizes the uniform thickness of the cuticula, the nearly uniform thickness of the hypodermis and the relation of the size and conical shape of the optic stalk to the amount of degeneration, as well as the histological structure of the degenerated eye. He also called attention to the relation of the axis of the cone, which is the terminal part of the optic stalk, to the axis of the stalk itself.

The most striking characteristics of the gross anatomy of the eyes of *C. setosus* and *C. pellucidus* are smallness, lack of pigmen-

tation and inconspicuousness. These features are shown in Figs. 1 and 2.

The eyes of all the blind crayfish examined are nearly covered by the rostrum, from a dorsal view, while the eyes of normal crayfish are only slightly concealed by the rostrum. However the eyes of the young blind crayfish are relatively larger than they are in the adult. The relative size of the eyes of *C. setosus* and *C. propinquus* (?) is shown in Figs. 2 and 3.

Size and pigmentation make the eyes of normal crayfish conspicuous. The eyes of blind crayfish are smaller and without

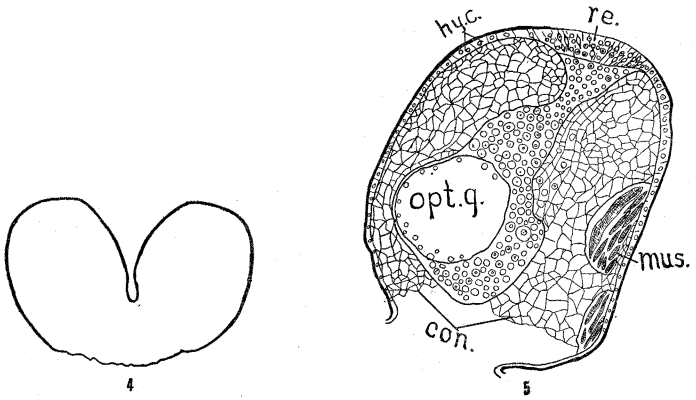


FIG. 4. Outline of the eyes of *C. pellucidus* 10 mm. long.

FIG. 5. Horizontal (longitudinal) section of the eye of *C. setosus*, with the cuticula removed.

pigment. The relative shortness of the optic stalk in the eyes of blind crayfish tends to make them inconspicuous.

The distal end of the optic stalk of the eyes of the blind crayfish examined is roundish or almost hemispherical in shape. Fig. 4 which shows this was made with the aid of a camera lucida, from a fresh specimen of *C. pellucidus*, 10 mm. long. The same general form of the eye is shown in photomicrographs *A* and *B*, which were made from a horizontal section of the eyes of *C. setosus*. In no case out of fifteen series of sections of the eyes of *C. setosus* and *C. pellucidus* have I found the exaggerated conical form figured by Packard and by Parker. Crayfish killed in Perenyi's fluid and kept in 85 per cent. alcohol for a few weeks

show considerable shrinkage of the connective tissue and after some months the cuticula shrinks. Dehydration and embedding also cause further shrinking. See photomicrographs *A* and *B*. The optic stalk may then approach the conical form observed by Packard and by Parker.

The cuticula of the eyes of *C. setosus* and *C. pellucidus* is usually smooth. Sometimes it is wrinkled by the fixer or preservative. These wrinkles may have led Newport to the conclusion that it is faceted. The main points of interest concerning the cuticula are; first, it is thinnest in that part of the optic stalk occupied by the cells of the vestigeal eye; second, it is laminated.

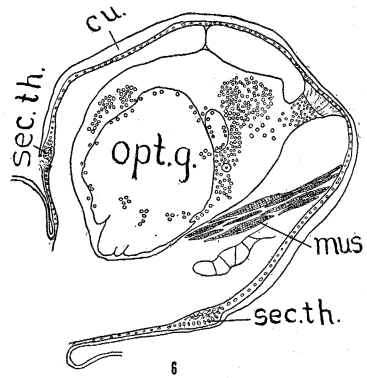


FIG. 6. Horizontal section of the eye of *C. setosus*, with the cuticula removed Made from a section near the one shown in photomicrograph *A*.

Sometimes the cuticula in *C. setosus* and in *C. pellucidus* is from two to three times as thick on the sides as it is on the anterior end or retinal region of the optic stalk. My photomicrographs *A* and *B* and Fig. 6 show that the cuticula is thinnest in the retinal region. According to Gilbert the average thickness of the retinal cuticula is 3.41 mm., while that of the sides of the stalk is 12.41 mm. This is quite contrary to Parker's statement that "The optic stalk is covered with a cuticula which is of uniform thickness."

It will be recalled that the cuticula is secreted by the hypodermis. The hypodermis which is of ectodermal origin becomes differentiated into the visual organ in Arthropoda. This differentiation consists of the thickening and invagination of the hypodermis.

The part of the degenerated eye of the blind crayfish which is of chief interest is the retinal hypodermis. Here the largest amount of degeneration has taken place. The optic ganglion, optic tract and brain show little or no signs of degeneration. The condition of these structures is well illustrated by photo-

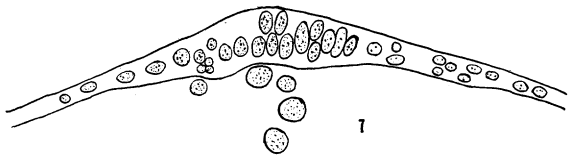


FIG. 7. A secondary thickening of the hypodermis from the antero-median part of an eye of *C. setosus*.

micrographs *B*, *C* and *D*. The optic nerves (Fig. 8 and photomicrographs *C* and *E*) connecting the retinular cells with the optic ganglion are also present but they are not as well developed as the above mentioned structures.

It is probable that when the embryology of the eye of the blind crayfish is worked out, we may be able to definitely identify the retinal cells shown in Fig. 8. The eyes of a *C. setosus* 15 mm. long show about the same amount of degeneration as the eyes of adults. The arrangement and general appearance of the retinal cells of the hypodermis, shown in Fig. 8, is comparable to an early embryonic condition found in the developing eyes of many Crustacea, the bee and other Arthropoda.

Parker states that the hypodermis in *C. setosus* is "very nearly uniform in thickness." I find that the retinal hypodermis in *C. setosus* and *C. pellucidus* is quite irregular as to thickness. Sometimes there are as many as three and four different thickened regions in a single section. These thickened places in the hypodermis are found at various places around the anterior end and the sides of the optic stalk. The principal and most common thickening is in the anterio-lateral part of the optic stalk, as is shown in Fig. 5 and photomicrographs *B*, *C* and *E*. Secondary thickenings are sometimes low on the sides of the optic stalk, as illustrated by Fig. 6 and photomicrograph *A*. Fig. 7 represents a type of the secondary thickenings. It was taken from a portion of the hypodermis along the anterio-median part of the right eye of *C. setosus*. The most highly developed or the least

degenerated of these thickenings are in the anterio-lateral or retinal portion of the optic stalk. This point is well illustrated in Figs. 5 and 8 and photomicrographs *B*, *C* and *E*.

The retinal region of the hypodermis has two or three distinct layers of cells, while the rest of the hypodermis has only one layer of cells, except in secondary thickenings such as are shown in Figs. 6 and 7 and photomicrograph *A*. The cells of the retinal hypodermis in *C. setosus* and *C. pellucidus* differ in size, shape and staining properties from the other cells of the hypodermis. My drawings and photomicrographs show that the hypodermis is considerable thicker in the retinal region than elsewhere. Here

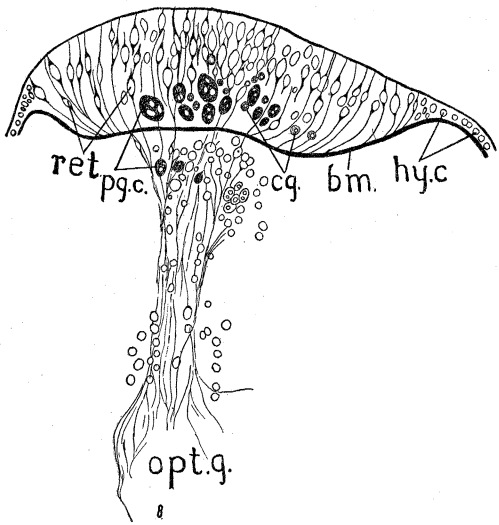


FIG. 8. Cell structure of the retinal region of the eye of *C. setosus* from a section similar to those of photomicrographs *B*, *C* and *E*.

again I differ from Parker who said of the hypodermis in *C. setosus:* "At least it is not thicker in the region of the retina than at many other places."

The ommatidium or ocellus (Fig. 9) is the unit of structure of the compound eyes of Arthropoda. The functional eye of *Cambarus* has four layers of cells in the developing retinal hypodermis; the corneagen, the vitrellæ, the retinulæ and pigment cells.

The diopteric structures of the eye, such as the lens, cone and

rhabdom are absent in the eyes of *C. setosus* and *C. pellucidus*. Some of the sensory cells are present even though they may be no longer functional. I believe we may feel reasonably sure of the identity of some of the cells found in these degenerated eyes.

In Fig. 8 there are at least three kinds of cells shown; (1) the large, oval, dark staining, granular cells with several nuclei, the "granular bodies," "degenerated representatives of the cones in the normal eyes" of Parker, (2) elongated cells or nuclei with fibers, and (3) small, round, granular cells with clear nuclei.

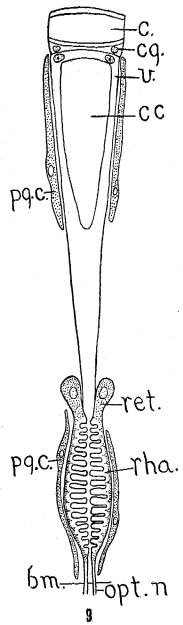


FIG. 9. The ommatidium of *Cambarus*. (After Watase.)

The large, oval, dark staining, granular cells with several nuclei are probably pigment cells as they are the only similar cells found on both sides of the basement membrane in the functional eyes as well as in these degenerated ones. Parker found "granular bodies" on the distal side only of the basement membrane and called them "degenerated representatives of the cones in the normal eye."

The elongated cells with fibers compare with the retinulæ of the functional eye. The retinulæ are the only cells with fibers in retina.

The small, round, granular cells with clear nuclei may be degenerated cone cells or the "undifferentiated hypodermal cells" of Parker. But most of these cells are too far removed from the cuticula to be "undifferentiated hypodermal cells" which have secreted the cuticula. The cuticula is thin in the retinal region. According to Watase, the sensory cells of the ommatidium secrete the cuticula. I am inclined to believe that the small, round, granular cells are degenerated cone cells.

Comparing the sections of the eyes of *C. setosus* and of *C. pellucidus* it is found that the eyes of *setosus* are little if any more degenerated than those of *pellucidus*. Irregularities are common in the retinal hypodermis of the eyes of these crayfish.

Whether the eyes of the blind crayfish have passed through a higher stage of development and then degenerated or whether

their development has been arrested at this stage, can be determined only by a study of the developing eyes.

However I believe that the degenerated eyes of *C. setosus* and *C. pellucidus* are instances of arrested development rather than examples of degeneration. The reasons for this belief are that the eyes as found in the adult have a cell structure which appears to be comparable to the developing eyes of Crustacea. The radiate arrangement of the retinal cells of the hypodermis, is suggestive of the developing ommatidium. Also the eyes of the young blind crayfish, *C. setosus* and *C. pellucidus*, show about the same amount of degeneration as the eyes of the adult.

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EXPLANATION OF FIGURES AND ABBREVIATIONS.

The tissue was fixed with Perenyi's fluid. The sections from which the drawings and photomicrographs were made were cut eight microns in thickness and stained with Haidenhain's iron hæmatoxylin. The drawings were made with the aid of a camera lucida.

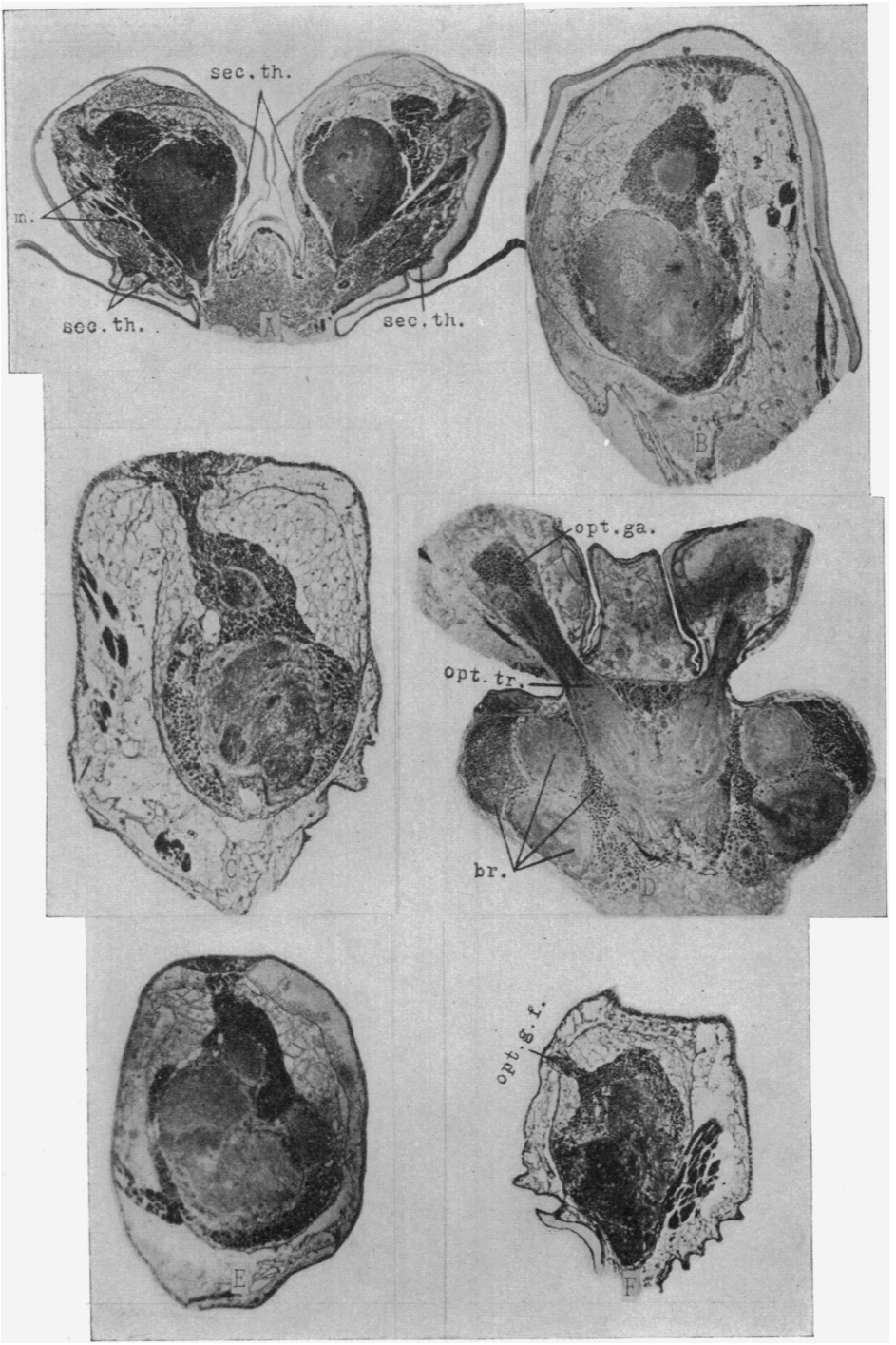
bm., basement membrane.
br., brain.
c., cornea.
cc, crystalline cone.
cg., corneagen cell.
con., connective tissue.
cu., cuticula.
hy. c., hypodermal cells.
mus., muscle.
opt. g., optic ganglion.
opt. g. f., optic ganglion fibers.
opt. n., optic nerve.
opt. tr., optic tract.
pg. c., pigment cell.
re., retina.
ret., retinulæ.
rha., rhabdom.
sec. th., secondary thickenings of the hypodermis.
v., vitrella.

PHOTOMICROGRAPH *A*. Horizontal section of the eyes of *C. setosus*.

PHOTOMICROGRAPHS *B* AND *C*. Horizontal sections of the eyes of *C. setosus*. *C* has the cuticula removed. The cuticula in *B* is thinner in the retinal than it is on the sides of the optic stalk. It is not as thick as it appears to be in the retinal region, due to the fact that it is wrinkled. It is also pulled loose from the underlying hypodermis, caused by the shrinking of the more delicate tissues.

PHOTOMICROGRAPH *D*. Horizontal section of the brain of *C. setosus*.

PHOTOMICROGRAPHS *E* AND *F*. Horizontal sections of the eyes of *C. pellucidus*. The cuticula has been removed. *F* has a tract of nerve fibers extending anteriomedianly towards the hypodermis, but there is no thickened portion of the hypodermis with which it is connected.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